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Scale Adaptation and Utilization in *Aesiocopa patulana* Walker (Lepidoptera, Heterocera, Tortricidae).[1]

WILLIAM BEEBE.

Department of Tropical Research, New York Zoological Society.

(Plates I & II; Text-figures 1 & 2).

[This is one of a series of papers resulting from the 45th and 46th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945 and 1946 under the direction of Dr. William Beebe with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.

[The characteristics of the research area are in brief as follows: Rancho Grande is located in north central Venezuela (10° 21′ N. Lat., 67° 41′ W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane cloud forest which covers this part of the Caribbean range of the Andes. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh water lake of Valencia and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity, during the expeditions, including parts of both wet and dry seasons, was 92.4%; the average temperature during the same period was 18° C.; the average annual rainfall over a 5-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details, see Beebe & Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were taken in the montane cloud forest zone, within a radius of 1 kilometer of Rancho Grande.]

About 9 o'clock on the evening of June 11 I was on the roof of Rancho Grande watching the onrush of hosts of moths as they siphoned in from the dark jungle and came to rest on the whitewashed wall, attracted by the brilliance of the electric light overhead. Close to my face there alighted a small brown, bell-shaped tortricid. After recording its alighting position, I collected it alive and later carried it to the laboratory with the intention of noting the resting position next morning. There intervened a phenomenon of egg-laying and defense adaptation which gave greatly increased interest to the moth.

She was enclosed in a small, round, glass-topped, glass laboratory dish, measuring 50 mm. in diameter by 25 mm. deep. When I left her at midnight she was resting quietly on the bottom. In the morning about 6 a.m. she was quiescent in the same position, while directly overhead, on the inside of the glass cover, were the eggs and their defensive barrier which she had deposited in the intervening six hours.

Subsequently the egg-laying tortricid (Cat. No. 46564) was identified by the kindness of Dr. J. F. Gates Clarke. On June 23 a second female was hatched from a naked pupa at Rancho Grande (No. 461190), and this was named by Dr. T. N. Freeman. Both proved to belong to the same species, *Aesiocopa* (or *Cacoecia*) *patulana* Walker. The locality of Walker's type was Oajaca (*sic*) in southern Mexico, and to this Dr. Clarke added localities in Central Mexico, Guatemala and Costa Rica. The present Rancho Grande specimens represent a considerable southward extension of the range, to north-central Venezuela.

EGGS: During the night of June 11 a mass of more than three hundred eggs was deposited in an almost circular form, singly around the periphery, doubling and trebling in depth toward the center. The mass measured 8.6 mm. across and .7 mm. deep. The collection was opaque, pale viridine green in color (Ridgway), with the individual eggs apparent by slightly curved outlines on the surface, and a series of scallops around the outer edge. There were sixteen to eighteen eggs across the widest part and about fifty around the outside. The general deposition arrangement was in concentric lines.

The whole flat mass was covered with a fairly thick but irregularly scattered nap

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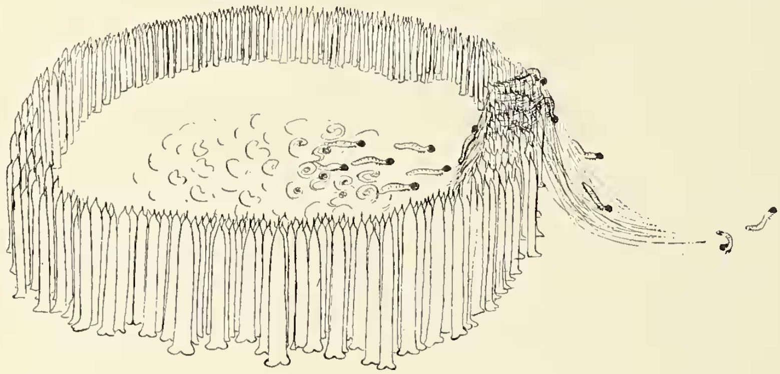
of very fine, short, colorless, transparent, needle-like scale-hairs, very difficult to see. Outside of the eggs, on the glass, there was a very narrow, irregular, ring of these scales as if they had fallen here by accident instead of on the eggs. They lay flat, facing in every direction, and the outer scattered fringe was about .75 mm. wide. The area bordering a single egg scallop contained fifty to seventy of these hairs. They were .20 to .25 mm. long.

Outside of these, beyond a perfectly clear space of 1.5 to 2 mm., there extended a second ring of wholly different scales. Viewed obliquely the egg mass looked like a flat, pale-green island in clear water, surrounded at a little distance by a dense palisade of stakes standing upright in the water.

This outer ring was a circle of scales. The ring was slightly broken at the bottom, an imperfection due unquestionably to the exigencies of the abnormal conditions of the glass container. Proof of this is provided by the actual presence of the missing scales, misplaced, flattened and scattered over a very small asymmetrical section of the eggs themselves. The ring was somewhat irregular as to width, 1.5 to 2 mm., and every scale was vertically on end and separate from its fellows. Each scale had a pale-brown, kidney-shaped basal expansion, forming a flat foot which must have been sticky enough to allow it to become fast and continue to support the scale absolutely vertically. A very few scales, having lost their bases, were lying flat. Each one was extremely thin, flat or slightly curved and wide, equally calibered throughout, except at the tip which changed abruptly into a fine, needle-like, sharp spine. The erect scales were so thin and straight that from above, almost nothing was visible but the expanded bases. The encircling palisade was from ten to fifteen scales in width, and the entire ring about 43 mm. in circumference. A conservative estimate, after several counts, gave a total of three thousand.

A vertical view showed the green egg mass surrounded by a brown ring of small kidney-shaped dots. An oblique sight brought the ring scales slowly into upright elevation, as unexpectedly as a stereoscopic photograph.

There is no doubt that this achievement on the part of a small moth is an adaptation of the most complex character. The method of denudation of her body of three thousand scales (in addition to the egg mat of thousands of hair scales), of the placing of the palisade scales in erect, orderly arrangement, separated by almost arithmetically exact spaces, and fastening into place, forms a complicated sequence, the evolution of which is beyond our comprehension.



TEXT-FIG. 1. Sketch of palisade scale ring with escaping caterpillars. (Drawing by Pamela Marmont).

Eight days after deposition, on June 19, each egg was seen to be filled with the body of the embryo. The head showed as a large black spot, while close behind it was a dark, rectangular area, the prothoracic dorsal scute of the hatched caterpillar. The jaws were extended in advance of the head, and each embryo faced outward toward the periphery of the egg circle. Two days later, on June 21, the whole egg mass had changed in color to dark olive. The width of the eggs was about .8 mm. I was worried about the dried aspect of the upper side of the eggs, so dissected out one larva, but it and all others in the vicinity wriggled healthfully.

LARVAE: The following day, June 22, eleven days after the eggs had been laid, I found that a third of the larvae had emerged and disappeared. The central part of the upper layer of the mass had emptied first. Even this hinted at a delicate but appreciable adaptation, for this upper layer of eggs must have been deposited last, *after* the lower layers, even if the interval had been only a few minutes, and now a much longer, as well as a reversed, period of time intervened between the hatching of the relative layers. Not a single first floor occupant had emerged, while most of the upper floor tenants had already left their glassy cells.

As I watched, two more newly hatched caterpillars appeared, walking back and forth. Soon both reached the outer rim of the eggs at the exact point nearest the source of light from the laboratory window. They crossed the clear space and began to investigate the edge of the palisades. One reared high and after feeling about a few times, strained upward and crept over the first two spikes. Then the second attempted it and both crossed with amazing speed. It was very evidently uncomfortable but over they went and swiftly humped themselves down the outer side, across the glass, and on lightwards.

I now watched a black pair of jaws which had just appeared, chewing upwards into view in the egg expanse. I started the stopwatch. In two minutes the caterpillar had gnawed a hole of his own caliber, pushed up and out, and began crawling. He completed a small circle, then turned toward the light, crossed the open take-off, mounted, crept across and reached the far side of the palisade in exactly two more minutes. In four minutes he had gnawed his way out of his egg, found and surmounted his first ontogenetic hurdle.

The palisade traverse bothered me. It was too easy, for the stakes were as erect, the points as sharp as ever. I made a slight shift in focus of the microscope lens and the mystery was no longer a mystery. A wide pathway over the lighted segment of the palisade was covered with the thinnest of thin silk webbing. The apparently casual weaving back and forth of the larval heads became significant. The speed and ease of crossing was explained by the soft approach ramp and the silk carpet over the top.

I now revolved the glass cover holding the egg mass, half a circle away from the light side. Closest examination of this former darkened section showed only a few stray strands of web. After a minute a second tier larva began to shred and tear his cell wall. When he had eaten through the wall of his particular egg he walked a short distance and then made quick work of a trapdoor in the roof, for the emerging of the earlier caterpillars had cleared a large space beneath the transparent, communal ceiling. The larva emerged in par and at once set out lightwards. As soon as he touched the first palisade he began weaving, but proved to be a pioneer, not merely adding a ratline here and there to the suspension bridge of preceding brethren. His was the hard way, he made slow progress, it was difficult going. On his posterior pair of prolegs he raised himself half way up a vertical scale, and with bent head wove the first warp of a silken path. The palisades were as strong and efficient as when they were first mysteriously planted by the parent moth and the larva would touch and flinch at each sharp point. Then he would pull back, reach down and draw out a strand of silk. This was wound muffler-like, forming a soft wad around the needle tip. Another step was taken, with much irritated jerking and twisting, and finally the hindmost pair of prolegs of the caterpillar gripped the very summit of the wadded spikehead. This provided a new periphery, enabling him to reach two further palisades.

An unfailing instinct held him straight on—the inevitable pull of the light. He never stopped or wavered. Close on the left the stakes thinned out, leaving a free little alley for some distance of the traverse, but he did not see or else ignored this easy but oblique path. He held straight on, travelling the shortest line which led directly toward the light.

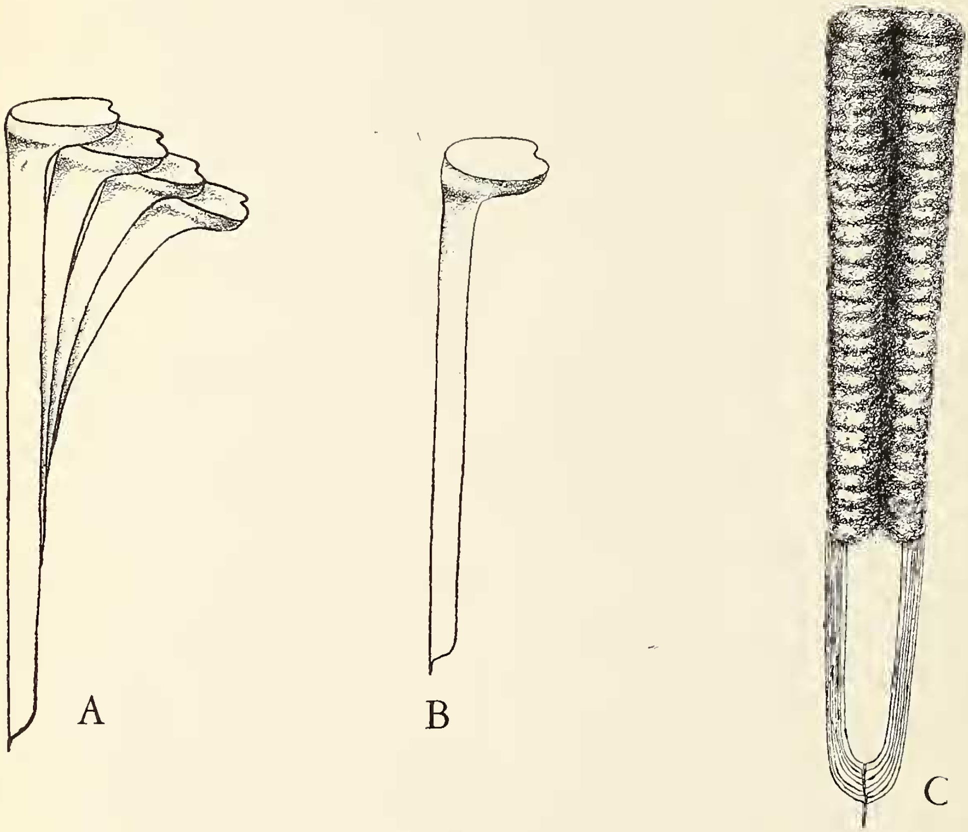
I now revolved the whole affair so that at this stage he was suddenly headed toward the dark side. But the formative positiveness of his phototropic instinct had done its part, and was now past history. He kept on and when free of the obstacle he humped full speed toward the darker direction.

I watched another larva emerge and do his palisade crossing and when he had reached the outermost rim of the glass, I touched and lifted him with the entangling hairs of a camel's-hair brush. He payed out several inches of web, dangling in midair, and I dropped him again on the egg mass. He righted himself, cut his rip-cord and began walking rapidly about. Now and then he met and crawled over another larva, or stopped for a moment at the touch of a black head arising from its cell. All the larvae hatching while he walked about—six altogether — went through their postnatal routine: all emerged, crossed the clear space, hopped the fence and started out full of directed energy. My returned caterpillar still roamed about. He would start off full tilt over eggs and bodies until he reached the palisade, feel about for a moment, then turn and step out in another diagonal, and again turn back. The last I saw of the confused caterpillar he was resting quietly close to the egg opening from which he had emerged. Five hours later he was still there and quite unresponsive to any effort to arouse him to activity. I had interfered with his set routine, his sequence of instincts; I had set back the time clock of his life and he refused to repeat and catch up again. Quite uninjured, he was again in the identical situation, with the same means to scale the obstacle, but he had yielded to the next item on the program, to walk, walk, walk until, under normal conditions, he probably would have arrived at the leaf which the equally blind instinct of his parent should have placed within his reach. Foiled in this he became obsessed with a meaningless quiescence. My ignorance meant his death, for even if I had not interfered with his routine I had no possible means of knowing which of the thousands of jungle plants growing about Rancho Grande was the one suited for his nourishment.

My final experiment was to reorient the egg mass so that the accidental opening in the outer palisade ring faced the source of light from the laboratory window. Four caterpillars hatched during the next few minutes and crept straight for the opening. One kept on with scarcely a second's hesitation. The other three interrupted their progress with six to twenty seconds of indefinite turning, twisting and reaching up and about. Two of the larvae halted close to the broken periphery. The other experienced his momentary confusion 20 millimeters beyond where the palisade would have been if the ring was perfect. It appeared "as if" seventy-five per cent. of the larvae experienced an instinctive expectancy of a barrier.

Source of the Palisade Scales: On the terminal portion of the abdomen of this tortricid moth is an extensive mass of specialized structures which I shall call palisade *sheaves* because each unit consists of varying numbers of palisade *scales*.

Their appearance is most difficult to describe. The most apt simile is the mass of basalt crystals which forms the so-called Giant's Causeway in Ireland. The palisade



Text-fig. 2. **A.** Four of the forty palisade scales telescoped in one sheaf. **B.** Lateral view of outer single scale of sheaf. **C.** Posterior view of a single sheaf, showing successive layers of scales.

sheaves form three-fifths of a steeply sloping cone, covering the whole of the ventral and lateral areas of the terminal abdominal segment. The remaining two-fifths occupy the flattened, dorsal portion. The diameter of the base of the cone is 2.2 mm. and the height 1.4 mm. These scales enclose the paired ovipositors ventrally and laterally, leaving the antero-dorsal aspect in direct contact with the more normally shaped lepidopteran scales of the rest of the abdomen.

Anterior to the ventral limits of the palisade sheaves is a dense, rough triangle of a solid mass of very small, hair-like scales, extending over a transverse area of 1.2 mm. These are the scales which form the fine nap overlying the egg mass.

Ventrally, the palisade sheaves on the undisturbed abdomen of the virgin tortricid, number about three hundred and the lateral extensions add some two hundred more, the total count being around five hundred. The hair-scale area slightly overhangs the bases of the anterior sheaves, which here lie almost flat, their heads directed posteriorly, with about half their length exposed. Posteriorly, in the direction of the ovipositors, the scales become more erect, bringing the expanded summits closer and closer together. At the time of utilization, there must be some muscular or other mechanism for erecting and leveling off the entire expanse of palisade sheaf tops.

The palisade sheaf count on the abdomen of the *parent* tortricid is about three hundred, considerably less than the total on the body of the reared, virgin moth. In the parent insect, however, the contraction of the shrunken, eggless abdomen has drawn down the tip of the body, so that many of the peripheral rows of sheaves are concealed, especially those that have been telescoped beneath the overhanging fringes of the matted hair-scales.

Even if we endow the parent moth originally with the full five hundred sheaves of the virgin female they do nothing to explain the three thousand extracted, individual palisade scales mounting guard about the eggs, each with a kidney-shaped base, indistinguishable from the tops of the abdominal sheaves here *in situ*. For days this remained a mystery, apparently solvable only by a refutation of the law that two bodies may not occupy the same space.

Finally, a single sheaf was freed from its bed and placed on a microscope slide. Pressure from a needle point solved the problem, for one by one, like the successive enveloping leaves of an endive stalk, palisade scales split off, until, instead of one, there were three and twenty, each, except in size, practically identical with the first, outermost shell which I had lifted from its place. A second sheaf revealed the fact that by means of the moistened tip of a needle it was possible to lift first the uppermost legume-shaped cap, together with its slender spine-tipped body, and then in turn all those beneath. A typical, first, uppermost scale measured .7 mm. in length. Scale number twenty-three was one half as long. We later found that extremes were as much as 3 to 1. In general shape all were similar, except that the terminal spine was relatively short on the first scale, gaining in length and slenderness on each succeeding one. It was difficult to remove from its bed a complete palisade sheaf. At the slightest pressure the successive scale layers bent slightly outward or sprang free. When one was finally isolated and examined, still partly *in situ*, it was found that the entire protruding length was bean-shaped in section. This shape was contributed by the vertical series of bean-shaped caps resting one upon another, externally visible only as a succession of rounded layers, with the concavity pattern continuing down one side.

The particular sheaf under consideration, when completely freed, showed the lower third of the anterior aspect quite open, marking the lower end of the pile of caps together with the exposed inner aspect of the lowermost scale. In this particular individual sheaf there were forty-one scales. This number of palisade scales in single sheaves varied from fifteen to forty-one, a reasonable average providing a total of twelve thousand five hundred scales for the use of the parent moth.

Allowing our egg-laying parent tortricid a full five hundred sheaves of scales, she must have utilized the six uppermost layers to build her circle of three thousand palisades.

METHOD OF DEPOSITION: Darkness, and especially the lack of any warning, combined to prevent any actual observation of the process, but a few facts give us meagre indications of a possible mode of deposition. The sheaves on the abdomen of the moth are so oriented that the incised or concave sides of the bean-shaped extremities are all directed posteriorly. A second fact is the presence of a series of shallow scallops around the periphery of the palisade ring, which are about abdomen width. In the third place, the direction of the concave sides of what are now the bases of the palisades are uniformly directed outwardly.

From these facts we can guess that after the deposition of the eggs, the moth stationed herself with head over the center of the egg mass and abdomen pointed outward. In this position the abdomen tip would reach a little way beyond the circular patch of eggs. A mucilaginous application of the ovipositors (or other source of viscidity) followed by a touch of the sheaves would result in the abstraction of the uppermost layer of scale heads and retention of the entire scales in an upright position on the adhesive surface.

A slight swivelling of the moth to left or right would make possible a repetition of the process, forming another scallop or segment in the growing ring of palisades. This is all sheer conjecture, but it seems within the realm of explanatory probability until we have an opportunity of observing the process at first hand.

ENEMIES: Against what particular enemies the palisade ring functions successfully we do not know. In the case of at least one mite and one ant, however, it justified its existence. When I was studying the structure under low power, a small pink mite appeared by accident on the glass and walked to the ring of scales. It made several attempts to climb but none to penetrate the stockade, then turned and kept on its slow way until it came to the broken section, felt about for a minute and walked away.

I deposited a small ant outside the ring and it ran at once to the outermost series, tried to push between, and then twice made a definite attempt to climb, failing in both. I dropped it in the center of the scales. It fell through them to the glass, squeezed between four pairs and then became completely trapped, wedged tightly. I did not want to leave it there, but in the rescuing process I upset three scales. All this is artificial yet significant evidence as to the possible value of the palisades.

SUMMARY: A female tortricid moth, identified as *Aesiocopa patulana* Walker, was taken at light on the roof of Rancho Grande in north-central Venezuela on June 11, 1946.

The same night, in a small glass laboratory dish, the moth deposited three hundred eggs, arranged in a flat, rounded mass. At a little distance from the eggs, the moth had erected a circular stockade of about three thousand pointed, elongate scales, standing upright upon enlarged bases firmly attached to the glass.

The caterpillars hatched on the eleventh day after the laying, and made their escape over the stockade of pointed scales by spinning a ramp and mat of silk. The direction of escape was always toward the strongest illumination.

The source of the scales was a group of four to five hundred sheaves near the tip of the abdomen, each containing from fifteen to forty of the pointed, palisade scales.

EXPLANATION OF THE PLATES.

PLATE I.

Fig. 1. *Aesiocopa patulana*, female, wings closed.

Fig. 2. *Aesiocopa patulana*, female, wings spread, showing shrivelled abdomen.

Fig. 3. End of abdomen of female moth showing 300 palisade sheaves in place.

PLATE II.

Fig. 4. Egg mass and circle of palisade scales, showing laboratory dish and the glass cover on which they were deposited.

Fig. 5. Vertical view of egg mass and protecting ring of palisade scales.

Fig. 6. Oblique view of eggs and scales, showing erect position of the three thousand palisade scales.